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**Progress Report
on
Biomechanics of the
Acoustico-Lateralis System in Fish**

[Navy Contract No. N00014-84-K-0164]

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The present goals of this research project are to (1) determine the characteristics of noise scattered by the swimbladder of the goldfish and the oscar, (2) develop a method to reproduce the scattered signal using signal generators, filters, and underwater transducers, and (3) measure the ability of the fish to discriminate this signal from simulated scattered noise. This research project has progressed in three major areas this past year: a more comprehensive literature review on fish hearing, improvements in the system used to measure the response of a fish's swimbladder to low frequency sound, and the acquisition of additional equipment needed for measuring the ability of a fish to detect scattered ambient noise.

Literature Review

A library of over 200 journal articles and 7 books relevant to fish hearing was compiled for reference. One result of this review was the drafting and successful defense of a Ph.D. thesis proposal.

Swimbladder Response

The majority of the effort in the past year was spent on refining the NIVAMS (Non-Invasive Vibration Amplitude Measurement System) to provide better accuracy and repeatability. In review, the NIVAMS uses low power continuous wave ultrasound to detect the motion of the swimbladder of a fish *in vivo*. The motion of the swimbladder introduces sidebands into the spectrum of the reflected signal. NIVAMS uses a HP 3585A spectrum analyzer to measure the relative amplitudes of the carrier frequency and these sidebands. From this data, the motion of the target can be determined.

The minimum measurable motion of this system is thought to be governed by two factors. The first involves the internal noise level of the spectrum analyzer. As the sidebands shrink due to decreased response and the inherent wavelength dependence (for a constant pressure stimulus to the swimbladder, the acoustic particle velocity decreases with increasing stimulus frequency), the signal to be measured ultimately approaches the noise level of the instrument. Since this internal noise level cannot be reduced, the signal level driving the ultrasonic transmitter was increased by 30 dB with a RF power amplifier. This consequently resulted in an approximately 30 dB gain in the reflected signal-to-noise at the analyzer, increasing the ability of NIVAMS to measure small displacements. Changes in the data acquisition programs were made to locate and measure the sidelobes more quickly and accurately.

At low stimulus frequencies (below 500 Hz), this effect is dominated by a second factor, which is thought to be caused by vibration of the ultrasonic transducers due to the low frequency excitation. The magnitude of both effects were measured by determining the

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response of a stationary target. This quantified the threshold of the measurement system, which was found to be at least an order of magnitude below the measured responses of swimbladders.

Early data has yielded several interesting results. One is that the resonant frequency of the goldfish's swimbladder differs significantly from that of a similarly sized air bubble (the resonant frequency is higher and the quality factor, Q , is lower). Another is that some goldfish have shown twin peaks in their resonance curves. X-rays of the subjects indicate that this response may be attributed to differences in the size of the anterior and posterior swimbladders. Data from the oscars has shown that their swimbladders resonate at much lower frequencies and higher Q s than those of goldfish of the same weight. Completion of this part of the project will involve collecting data on a significant number of goldfish and oscars to characterize the frequency response of their swimbladders.

Response to Scattered Ambient Noise

The second and third parts of this project follow the completion of the first. Presently, equipment is available to reproduce single peaked scattered signals using a noise generator, filters, and a spherical underwater transducer. The scattered ambient noise experiment station is currently being revamped with additional hardware to increase computer control.

In the first generation system, the experiment was run by a dedicated microprocessor controller. The output of this system was a paper tape EEG of the subject's heartbeat and markers indicating trials. The first modification was to replace the paper recorder with a waveform recorder and a general purpose computer, so that data collection was performed on-line. Next, the microprocessor controller will be replaced by a computer controlled switching system. With this, the computer will be able to run trials, collect data, and interpret responses. Most of the equipment necessary for this conversion has been procured. Completion of this part of the project will involve connecting the hardware, developing and testing the software, and collecting data on a significant number of goldfish and oscars to characterize their ability to detect scattered ambient noise.

Publicity

This project has generated a significant amount of media interest including articles in the Wall Street Journal, Mechanical Engineering, Research & Development, the Atlanta Journal-Constitution, and several Georgia Tech magazines and bulletins. The most surprising was a full Sunday comic strip by Mark Trail.

- Thomas N. Lewis

ABSTRACT

Fish have evolved a complex passive system for the detection of acoustic pressure and particle motion that rivals any man-made system. Since the frequency range of best sensitivity for the fish ear occurs where ambient noise is high, it may be assumed that the fish is using the ambient noise to its advantage. Rogers has presented a hypothesis that one fish could perceive nearby fish by recognizing the scattering of the ambient noise by other swimbladders. The swimbladder, acting like an air bubble, resonates in the ambient noise field, scattering significant amounts of acoustic energy. This characteristic scattered noise could allow for the detection and identification of the scatterer by the receiver.

Two experiments will be performed on goldfish and oscars to examine the basic premises of this hypothesis. The first experiment will characterize the scattering of sound by a fish by measuring the frequency response in vivo of the swimbladder using a continuous wave ultrasound measurement system. A second will use classical heart rate conditioning to determine if a fish could sense a similarly shaped filtered noise signal against a background of ambient noise. The results of this research may help shed light on the biological relevance of hearing in fish.



Statement "A" per telecon Dr. Bernard J. Zahuranec. Office of Naval Research/
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TABLE OF CONTENTS

| | |
|-------------------------------------|----|
| INTRODUCTION | 1 |
| BACKGROUND | 4 |
| The Fish Ear | 5 |
| Acoustic Stimulation | 8 |
| Swimbladder Resonance | 11 |
| Masking | 12 |
| PRELIMINARY EXPERIMENTS | 14 |
| Swimbladder Resonance | 14 |
| Response to Scattered Ambient Noise | 17 |
| PROPOSED RESEARCH | 21 |
| Swimbladder Resonance | 21 |
| Response to Scattered Ambient Noise | 22 |
| BIBLIOGRAPHY | 23 |

INTRODUCTION

Fish have evolved a complex passive system for the detection of acoustic pressure and particle motion that rivals any man-made system. Since the frequency range of best sensitivity for the fish ear occurs where ambient noise is high, it may be assumed that the fish is using the ambient noise to its advantage.

The perception of auditory space is of greater biological significance than the ability to communicate by vocalization, since all vertebrates have adaptations for spatial hearing, whereas only a few have found the ability to vocalize (Fay, 1988). Fay suggests that the primary function of the auditory system in most animals is to help form a three-dimensional image of the local environment. Perceiving objects in the environment involves separating their stimuli from the surroundings.

In order to survive, fish must be able to detect, classify, and localize relevant objects underwater in the presence of the ambient noise (Rogers and Cox, 1987). These objects include aquatic animals that can be either friend (conspecifics for schooling and mating) or foe (predators or prey). Rogers (1986) has presented a hypothesis that one fish could perceive nearby fish by recognizing the scattering of the ambient noise by other swimbladders. The swimbladder, acting like an air bubble, resonates in the ambient noise field, scattering significant amounts of acoustic energy. This characteristic scattered noise could allow for the detection and identification of the scatterer by the receiver.

Behavioral studies have shown that fish are able to discriminate differences in sound source location in three-dimensional space. It has been demonstrated in the cod (*Gadus morhua*) that (1) a fish can be conditioned to discriminate between different sound sources with minimum audible angles ranging from 2 to 20 degrees in azimuth or elevation

(Chapman and Johnstone, 1974; Hawkins and Sand, 1977), (2) the otolith organs of the ear are probably responsible for this behavior, (3) fishes are capable of sound source distance discrimination (Schuijf and Hawkins, 1983) and (4) they can solve back-front and left-right (180°) ambiguity (Schuijf and Buwalda, 1975; Popper and Fay, 1984). Solution to the 180° ambiguity demonstrates the ability of the fish ear to use both acoustic pressure and particle motion information.

Noise ultimately determines the detectability of any signal to which a fish may respond (Fay, 1974). In a noisy environment, signal detection becomes a complex discrimination problem. Decreased intensity thresholds below noise levels are not as crucial to signal discrimination as are mechanisms for the complex processing and analysis of the signals received.

Behavioral and electrophysiological research has demonstrated and quantified some of the complex auditory processing ability of the goldfish (*Carassius auratus*), including absolute detection thresholds, frequency discrimination, intensity discrimination, directional discrimination, temporal summation, complex spectrum discrimination, temporal discrimination and resolution, and auditory filter functions (see Hawkins, 1981). The data suggests that the capacity for auditory information processing, the detection of signals in noise, and the simultaneous and successive analysis of frequency of the fish auditory system do not differ significantly from those of the mammalian systems (Fay, 1978). Therefore the mechanisms responsible for the analysis may be the same in fishes and mammals even though the form of these ears are completely different. Currently we know a great deal more about the function of the complex and specialized structure of the cochlea than about the relatively simple acoustic receptor in fish (Tavolga, 1974).

One species of vocalizing fish has shown habituation to the presence and activities of neighboring conspecifics within its own territorial boundaries. Males of the bicolor damselfish (*Pomacentrus partitus*) are able to recognize individuals solely through

identification of the unique characteristics of their neighbors' vocal sounds (Myrberg and Riggio, 1985). Proper sound source direction was also found to be important in recognition, indicating the ability to spatially map acoustic information.

The purpose of this proposed research is to determine the capacity of a fish to detect the scattering of sound by another fish from the other's resonant swimbladder. The first task will involve measuring the characteristics of the acoustic signal scattered by the swimbladder of a fish. Next, this signal will be synthesized in a laboratory aquarium. The last task involves determining another fish's ability to detect this scattered ambient noise signal.

Although not conclusive, the results of this research may help shed light on the biological relevance of hearing in all fish. The more an animal knows about its environment, the better are its chances for biological success (Kamil, 1988). This proposed research will only indicate the ability of a fish to *sense* another through scattered ambient noise. The fish knows other fish are around if, after sensing, it is able to change its behavior upon identification by exhibiting the proper response (fleeing from predators, for example). If fish know more about their surroundings through input from their auditory system, then hearing is biologically relevant.

The results of this research may also prove useful to others who need to detect, identify, and localize relevant objects in the undersea environment. The fish's ability to extract acoustic information in the presence of ambient noise using its tiny sensors is unrivaled. Equally impressive may be their prowess in finding resonant structures underwater.

BACKGROUND

The underwater environment is a complex superposition of fluid motions and pressure disturbances, only a few of which result from propagating sound waves. Evolving underwater, fish have crafted specialized receptor organs to detect water motion and pressure disturbances. But there are no clear lines separating the detection of acoustic particle motion and acoustic pressure from the other mechanical disturbances just as there are no definite delineations of which organs are responsive to which stimuli.

Sound detection in fishes is thought to involve both the inner ear and the lateral line. The lateral line detects the spatial and temporal patterns of relative motion between the water environment and the surface of the fish (Platt et al., 1989). Its bandwidth spans from below 1 Hz to above 250 Hz (Popper, 1983), so the lateral line is responsive to pure hydrodynamic water motions as well as those caused by a true sound source. But since its threshold for motion detection is much higher than the inner ear's, the lateral line's contribution to hearing is relatively unimportant and will be ignored in this proposed research.

The first obvious question for researchers to answer was whether fish could hear. Bigelow (1904) was the first to show that goldfish respond in a definite manner to sound vibrations in water, disputing an earlier assertion that fish could not hear. In his experiments, Bigelow observed the response of normal goldfish to sound in an aquarium. Then he surgically severed the fifth and seventh nerves, the lateral line nerves, and the spinal cord close to the medulla, effectively desensitizing the skin and lateral line. These fishes reacted to sound the same as normal fish. In other fishes, only the eighth nerve (leading to the ear) was cut, and they didn't react to sound at all. Therefore, he concluded that goldfish could hear, and the inner ear was probably responsible.

The Fish Ear

Among the more than 20,000 species of fish, there is considerable structural and functional diversity in the inner ear and its peripheral accessories (Platt and Popper, 1981; Popper, 1983). Although there is no typical fish ear, a few basic morphological and ultrastructural patterns recur in taxonomically diverse fish groups (Popper and Coombs, 1982). The superorder Ostariophysi, for example, are distinguished by their specialized auditory structure, the Weberian ossicles. Nonostariophysines may or may not have other special connections between the swimbladder and the ear.

Dijkgraaf (1960) considered the Ostariophysi (the goldfish, catfish, minnows, and relatives) sound specialists due to the presence of their Weberian ossicles. The ossicles are a linkage of bones mechanically coupling the swimbladder to the fluid system of the inner ear.

The fish ear serves many purposes. The inner ear has evolved to function in controlling posture, locomotion, and eye stabilization as well as in the detection, analysis, and localization of underwater sounds (Platt et al., 1989). The otolith end organs of the inner ear respond to static tilt and to vibrations and sound from 0.01 to more than 5000 Hz in some fish species (see Popper and Fay, 1984). The swimbladder also has various functions in different fish. It serves in respiration, in the provision of buoyancy, in the detection of pressure changes, including sounds, and in sound production (Alexander, 1966).

The fish ear is a paired membranous system of contiguous fluid filled ducts and sacs consisting of two parts, the *pars superior* and the *pars inferior* [Fig. 1]. The *pars superior* consists of the utricle, the semicircular canals and their associated ampullary regions, and the macula neglecta. In most species the *pars superior* is thought to only be involved with detection of gravity and linear and angular acceleration (Lowenstein, 1971). An exception to this occurs in the

clupeids where the utricle was shown to be the major hearing organ (Blaxter et al., 1981).

The *pars inferior* consists of the other two otolithic organs, the sacculus and the lagena. There is considerable interspecific variability in the general shapes of the two organs, the interconnections between the sacculus and lagena, and the size and shape of the otoliths (Fay and Popper, 1980). The otolith is a calcium carbonate stone that is three times as dense as water. The saccular otoliths have complex and distinct species-specific shapes, while the lagenar otoliths are more commonly shaped (Popper, 1977).

The sensory epithelium of the otolithic organs, the macula, is overlaid with sensory and supporting cells. Some parts of a macula may be covered by the otolith within a gelatinous membrane, while other parts may be covered by only the membrane (Platt, 1977). The membrane is thought to act as an elastic coupling between the otolith and the sensory cells on the macula (Rogers and Cox, 1988).

The basic receptor element on the macula of the inner ear is the mechanosensory hair cell (Platt, 1983). Extending into the membrane from the surface from each hair cell is a bundle of microscopic hairlike processes [Fig. 2]. This bundle contains 20 to 80 processes called stereocilia and one true cilium, the kinocilium. The adequate stimulus for response from individual hair cells is bending of the cilia and is highly directional. Bending of the cilia triggers changes in the polarization of the cell: towards the kinocilium causes maximum depolarization, away causes hyperpolarization, and orthogonal to this axis yields no response. Bending off axis results in a cosine function response (Flock, 1971). This directional response results in changes in spike activity in the connecting afferent nerve fibers.

Hair cell orientation maps of the otolithic organs of the goldfish show that the macula has two oppositely oriented cell groups that can be separated by an unbroken line [Fig. 3] (Platt, 1977). Typically, the

hair cells in nonostariophysine saccule macula are divided into four orientation groups (Popper and Coombs, 1982; Saidel and Popper, 1983). The anterior region of the macula has two horizontally opposed groups, one directed anteriorly and one posteriorly. The other two groups are on the posterior region, oriented opposed dorsally and ventrally.

The innervation of the saccular sensory epithelium by branches of the eighth nerve show similar regionalizations (Saidel and Popper, 1983). The posterior saccular branch innervates the mid-region and the caudal end of the macula where the vertically oriented hair cells are located. The anterior saccular branch innervates the rostral region where the horizontally opposed hair cells lie. Each branch of the eighth nerve divides many times before it reaches the epithelial region. Individual axons terminate on several hair cells.

Sound is detected in most fish by the inner ear; but other peripheral structures may respond to sound and transfer acoustic energy to the ear. Von Frisch (1938) was the first to point out that the swimbladder in many fish could function as an accessory hearing organ, scattering incident sound energy with locally higher particle displacements.

In the goldfish and typical of other fish in the family Cyprinidae, the swimbladder consists of anterior and posterior sacs separated by smooth muscles (Alexander, 1966). Only the anterior sac is constructed with two walls. The inner wall (tunica interna) is whole while the outer one (tunica externa) has a longitudinal slit in it. Separating the two walls is a network of oily connective tissue, allowing the walls to slide freely over one another. The internal pressure of the gas in the sac keeps the tunica interna taut.

The Weberian ossicles (tripus, intercalarium, and scaphium) are derived from the anterior vertebrae (Alexander, 1966). The tripus is the most posterior, attaching to the tunica externa at the edge of the slit. Next is the intercalarium and then the scaphium, all connected

by a series of ligaments. When the swimbladder expands during the rarefaction phase of an acoustic wave, the tunica interna stretches, but the tunica externa does not, because of the slit. The edges of the slit move apart and the ossicles rotate forward due to the tension in the connections from the ossicles to the vertebrae (Popper, 1971). As the swimbladder contracts, the ossicles rotate back as the edges of the slit are moved together by elastic recoil of ligaments which connect the tripodes to processes of the fourth vertebra.

The scaphia are incorporated in the walls of a central fluid-filled cavity, the sinus impar (Alexander, 1966). The sacculi of the two ears are connected by a transverse canal. A posterior diverticulum of this canal, the sinus endolymphaticus, projects into the cavity of the sinus impar. It has a very thin wall. When the ossicles move forward, the scaphia press on the sinus impar, driving the fluid in it forward, compressing the sinus endolymphaticus and displacing fluid from it into the sacculi. This is possible because there is a flexible region in the saccular wall. The saccular otoliths bear wing-like projections which lie in the path of the endolymph movements caused by the Weberian ossicles. Therefore, motion of the ossicles due to the passage of sound waves causes movements of the saccular otoliths and thus stimulates the saccular hair cells.

In general, species in which the swimbladder and inner ear are closely coupled seem to perform 'better' than other species without such relationships in a number of auditory tasks, including simple sound detection and more complicated tasks related to frequency analysis. While some of these capacities are related to the pressure-transducing properties of the air filled swimbladder others may not be (see Coombs and Popper, 1982).

Acoustic Stimulation

The passage of an acoustic wave can be characterized by a change in a state variable (pressure, density, temperature) or a motion

variable (displacement, velocity, acceleration) and can be completely described by the field of any one (Rogers and Cox, 1988). The detection of at least one of these variables through either direct or indirect methods allows a fish to hear. It is now believed that the otolithic organs respond directly to the particle motion associated with sound waves and that many fish with swimbladders can indirectly sense the pressure fluctuations. The Weberian ossicles are thought to improve the coupling of the swimbladder to the inner ear, improving the sensitivity to acoustic pressure.

Fay and Popper (1974) calculated that for the goldfish the particle displacement at behavioral threshold is between 2 and 50 angstroms. They determined that for 'natural' situations, the fish would respond to sound pressure impinging upon the swimbladder before particle motion vibrating the head. But by removing the swimbladder, the only functional mechanism for stimulation is motion.

For the goldfish, it seems that information about the axis of particle motion is better represented in the profile of most active fibers within the lagena rather than in the saccule or utricle (Fay, 1988). The distribution of stimulus direction for best neural response in the saccule correlates well with the axis of the scattered pressure wave from the swimbladder. By recording microphonic potentials, Sand (1974) also demonstrated this in an unspecialized fish, the perch (*Perca fluviatilis*).

Van Bergeijk (1967) referred to the swimbladder as a secondary source of sound, radiating its own pressure and displacement fields when subjected to sound pressures. The resonant swimbladder amplifies the particle motion in the nearfield of the scattered sound.

To examine the relation of the pressure stimulus to the velocity stimulus, Buwalda and van der Steen (1979) performed experiments on cod using four opposing underwater sound projectors in a cylindrical tank. By manipulating the direction of the particle motion in the horizontal

and vertical planes and the ratio of the pressure to velocity, they demonstrated that at a low p/v ratio (high velocity), the sensitivity of the anterior part of the saccular macula was similar to the results from Sand (1974), but at higher ratios, the response was omnidirectional. These results indicate the ability of the pressure signal to overwhelm the directional velocity signal.

Poggendorf (1952) found that the threshold sound pressure of the ostariophysine bullhead (*Ictalurus nebulosus*) increased by 30 to 40 dB after removal of the tripus of the Weberian ossicles, although the shape of the auditory curve remained the same. From his data, he concluded that the amplitude of vibration in the labyrinth constituted the adequate stimulus for the sensory cells of the sacculus and lagena. This vibration was due to the swimbladder, so that the shape of the threshold curve depends on the resonance characteristics of the swimbladder.

Many species of fish have shown the ability to discriminate frequencies (Hawkins, 1981), although no mechanism for frequency discrimination is obvious in the form of the ear. Fay and Ream (1985) found that individual saccular nerve fibers of the goldfish can be grouped into four categories based on tuning and best frequency: (1) untuned, (2) low frequency (<120 to 290 Hz), (3) mid-frequency (330 to 670 Hz), (4) high frequency (790 to 1770 Hz). The frequency selectivity of these fibers act as bandwidth filters reducing broadband noise to lower detection thresholds for narrow band signals. The dynamic range for best sensitivity of separate saccular fibers is over 55 dB within individual goldfish (Fay and Ream, 1985).

An interesting model of the processing of acoustic signals in fish has been presented (Popper et al., 1988; Rogers et al., 1988). Their hypothesis assumes that the response of the saccule and lagena to direct and indirect acoustic motion can be decomposed into the directional information on the direct particle motion and pressure information.

This signal processing is thought to occur in the wiring of the eighth nerve fibers to the hair cells.

Swimbladder Resonance

Most of the previous work on the scattering of sound by the swimbladder has been concerned with the measurement of acoustic target strength for the estimation of quantity, size, and species of fish by commercial fishermen and marine biologists using sonar or echo-sounders. Others have made direct measurements of the motion of the swimbladder due to sound waves to study its effect on the hearing in fish. As a damped air bubble, the swimbladder resonates at a particular frequency and bandwidth based on its size, shape, and the characteristics of the surrounding tissue.

Experimental studies on the scattering by the swimbladder in fishes includes the work of McCartney and Stubbs (1971), Sand and Hawkins (1973), and Lovik and Hovem (1979), who used ring hydrophones to measure the resonant behavior of the swimbladder for various species and sizes of fish. In all of those experiments, it was shown that the resonance frequency and the broadness of the resonance curve (as characterized by Q , the quality factor) were significantly different than those of an air bubble in water; the resonance frequency of the swimbladder was higher and the Q lower. The majority of the scattered sound by intact fish was attributed to only the anterior portion of the swimbladder since the wall of the posterior sac is very much less extensible than that of the anterior sac (Alexander, 1959a).

Using a photocell, Poggendorf (1952) directly measured the oscillations from the anterior swimbladder of a minnow (*Phoxinus laevis*) that had been dissected out from the body. These excised swimbladders were found to have resonant frequencies coincident with those of similarly sized air bubbles with only a slight increase in damping.

By leaving the swimbladder in an anesthetized fish, Tavalga (1964) reported finding much higher damping using a contact microphone but cited only minimal data. Popper (1974) measured the response of the swimbladder by inserting a 0.5 mm probe coupled to a microphone into the anterior chamber of a dead goldfish. Results showed that the response of the swimbladder was flat from 50 to 2000 Hz, indicating extremely high damping. Both of these results were compromised due to the addition of the transducer to the swimbladder.

Cox and Rogers (1987) developed a technique to measure *in vivo* the motion of the swimbladder noninvasively using ultrasound. A comparison of *in vivo* and *post mortem* frequency response curves from early results showed the necessity of working with live subjects. This measurement system will be used in the proposed research.

Masking

The underwater environment is characterized by levels of natural and man-made noise. Any signal to be detected underwater will be masked by this ambient noise. Masking refers to "the process by which the threshold of audibility for one sound is raised by the presence of another (masking) sound" (American Standards Association, 1960). Determining the physical parameters that affect masking may elucidate functional aspects of the fish ear.

Using classical heart rate conditioning, Buerkle (1968) measured the pure tone threshold of the cod (*Gadus morhua* L.) to a background noise field of an octave band of noise centered around the test frequency. Up to 283 Hz, the signal-to-noise thresholds were constant (around 20 dB) at different background noise levels and different frequencies. Later (Buerkle, 1969), noise maskers centered around frequencies above and below the signal frequency were shown to be less effective than maskers of the same intensity at the signal frequency. This indicated the existence of auditory filters in the hearing of the cod. Similar results were later obtained for other species of fish: the

goldfish, *Carassius auratus* (Fay, 1974; Tavalga, 1974), the pinfish, *Lagodon rhomboides* (Tavalga, 1974), the African mouthbreeding cichlid, *Tilapia macrocephala* (Tavalga, 1974), and the blue-striped grunt, *Haemulon sciurus* (Tavalga, 1967).

The level of masking changes when signal and masker come from different directions (Chapman and Johnstone, 1974; Popper, 1983). For angular separations between tone and noise sources greater than 10 degrees, there was a significant decrease in the mean signal-to-noise ratio of about 7 dB. The same masking level differences were obtained for all angles between 45 and 180 degrees. This is an example of the cocktail party effect in fish, showing its ability to use directional information to differentiate signals from noise when the source of the signal is spatially separated from the source of the noise (Fay, 1988).

PRELIMINARY EXPERIMENTS

Two different experiments were performed to examine the basic premises of this proposed thesis. The aim of the first experiment was to characterize the scattering of sound by a fish by measuring the frequency response *in vivo* of the swimbladder. The goal of the second was to determine if a fish could sense a similarly shaped filtered noise signal against a background of ambient noise.

Swimbladder Resonance

The recently named NIVAMS (Non-Invasive Vibration Amplitude Measurement System) was developed to measure the motion of the internal organs of the peripheral auditory system in goldfish (Cox and Rogers, 1987; Cox, 1987). NIVAMS works due to the mismatch between the acoustic impedance of a vibrating structure and its surrounding media. The air-filled swimbladder has a much lower acoustic impedance than the surrounding water while the impedance of the otoliths and Weberian ossicles is higher.

The NIVAMS uses low power continuous wave ultrasound to probe *in vivo* the body of a fish, as shown in Figure 5. A transmitted high frequency sound wave is reflected by any impedance mismatch in its path. If the target is already in motion due to a low-frequency excitation, then sidebands at the sum and difference frequencies of the high and low frequencies are introduced into the spectrum of the reflected signal. By measuring the relative amplitude of these sidebands to the high frequency component of the reflected signal, the amplitude of the low frequency vibration can be calculated (Cox and Rogers, 1987).

With the present system, vibration induced sidebands with amplitudes 0.0001 times that of the carrier can be detected. Using a tuned 20 MHz transmitter, displacements on the order of 12 angstroms can be discerned. By crossing the axes of the sound beams of the

spherically focused transmitter and receiver, a spatial resolution of 0.28 mm in focal point diameter and 0.80 mm in depth was obtained (Cox and Rogers, 1987).

The *in vivo* response of the swimbladders of two goldfish measured with the NIVAMS is shown in Figure 6 (Cox and Lewis, 1987). The ordinate of the graph is relative motion, indicating the amplification of the swimbladder's displacement (or velocity or acceleration) over the acoustic particle displacement. The dashed line represents a 33 gram fish with a resonant frequency at 1400 Hz and a quality factor of 2. The solid line depicts a larger fish of 43 grams resonant at a lower frequency (1300 Hz) and a similar quality factor (1.7).

The curves show that the swimbladders of these fish scatter sound like a damped harmonic oscillator. The resonant frequencies measured correspond reasonably well with predictions obtained using the model of Andreeva (1964).

In this model, the swimbladder of a fish was assumed to be a spherical air bubble with the fish's body a visco-elastic matrix characterized by its complex shear modulus $\mu = \mu_1(1 + i\mu_2)$. Since the dimensions of the swimbladder are much smaller than the wavelength of sound in most of the fish's hearing range, the swimbladder was described as a lumped parameter system. This lead to the following equation for the resonant frequency (Andreeva, 1964):

$$f_0 = \frac{1}{2\pi R} \left[\frac{3\Gamma P + 4\mu_1}{\rho_w} \right]^{0.5} \quad (1)$$

where Γ is the ratio of specific heats for the gas in the bubble, P is the static pressure, ρ_w is the density of the water, and R is the radius of the bubble.

The quality factor, Q , for this model can be calculated from (Andreeva, 1964)

$$\frac{1}{Q} = \frac{2\pi f_0 R}{c} + 3(\Gamma - 1) \left[\frac{h_0 P_0}{4\pi f_0 P} \right]^{0.5} + \frac{\mu_1 \mu_2}{\pi^2 f_0^2 R^2 \rho_0} \quad (2)$$

where c is the speed of sound in water and h_0 is the thermal diffusivity of the gas at pressure P_0 (1 atm). The first term represents the radiation damping, the second thermal damping, and the third viscous damping. In this application, the viscous term dominates, and the thermal damping can be neglected.

The difficulty in using this model is in the precise determination of the shear modulus. Andreeva (1964) presented tentative measurements of $\mu_1 = 10^5$ to 10^6 Pa, and $\mu_2 = 0.2$ to 0.3 with no additional comment. Lebedeva (1965) measured directly the complex dynamic shear modulus of muscle tissue specimens for one freshwater and several saltwater fish, demonstrating that although it was similar for different species, the shear modulus is a strong function of specimen fiber orientation and frequency. By inverting equations 1 and 2 and using the measured values for f_0 and Q , estimates for the shear modulus, μ_1 , and the loss factor in shear, μ_2 , can be made.

By assuming that the volume of the swimbladder is 8% of the goldfish's total volume (Alexander, 1959b), an estimate of its size can be made from

$$(4\pi/3)R^3 = 0.08M_f/\rho_f, \quad (3)$$

where M_f is the mass of the fish and ρ_f is its density. Since the goldfish has a swimbladder divided into approximately equal anterior and posterior chambers, the estimated volume for the anterior portion was

half the total. For the 33 gram fish, this calculated to $R = 6.8$ mm, and for the 43 gram fish $R = 7.4$ mm.

The dynamic complex shear modulus was then calculated, $\mu_1 = 7.9 \times 10^5$ Pa and $\mu_2 = 0.52$ for the smaller fish and $\mu_1 = 8.1 \times 10^5$ Pa and $\mu_2 = 0.62$ for the larger fish. Lebedeva (1965) measured values of this order of magnitude for the shear modulus, but not for the loss factor, as his results spanned $0.12 < \mu_2 < 0.40$. Estimates of the shear modulus from the experimental results of McCartney and Stubbs (1971) and Lovik and Hovem (1979) were also in the same range.

Comparing these results, this study indicates that there is more damping in the swimbladder of a living fish than what is predicted by Andreeva. This may be attributed to the additional structure in the fish's body.

Response to Scattered Ambient Noise

A second preliminary experiment, shown in Figure 7, was conducted to show that goldfish could detect simulated scattered ambient noise in a noise masker (Rogers et al., 1989). In this experiment, threshold of the scattered noise as a function of distance from the fish was determined using classical heart rate conditioning.

Otis, et al. (1957) were the first to demonstrate classical heart rate conditioning in goldfish. Since then it has been used to measure the intensity thresholds and other discrimination capabilities of various fish (Buerkle, 1967, 1968; Chapman and Johnstone, 1974; Chapman and Sand, 1974; Offutt, 1971; Sand and Karlsen, 1986).

In this experiment, two comet goldfish (approximately 14 cm in standard length, 100 grams) were tested. The fish were held in a fixed location in a 50 gallon aquarium using a restrainer. The tank was covered on all sides and a constant light source was added from the top to eliminate any visual clues.

The simulated ambient noise was created by a noise generator (20-20,000 Hz white noise) and amplified to 0.595 V rms. The noise signal was input to a J-9 underwater transducer suspended in the test tank [Fig. 2]. The simulated scattered signal was the same white noise selectively attenuated, bandpass filtered between 680 and 720 Hz, and amplified. This filtered signal was sent to a small spherical transducer that could be positioned at various locations near the restrained fish.

The spherical transducer produced an acoustic signal simulating the scattering of a swimbladder resonant at 700 Hz, corresponding to a scattering cross section of about 10 sq. in. and a fish size of 15 in. in length. The bandwidth of the scattered signal was about 150 Hz.

A simulated scattered noise signal was created instead of having another live fish scatter the ambient noise to prevent detection through other sensory stimuli. If another fish was used, it would have to be surrounded by an acoustically transparent barrier impervious to possible visual, chemical, and hydrodynamic cues.

For the heart rate measurement, electrodes were fabricated from no. 8 stainless steel needles coated with polyurethane except at the tips. Two were inserted through the ventral side of the fish, one on each side of the heart (Roberts et al., 1973). The electrodes were adjusted in insertion depth for maximum signal. This ECG signal was amplified and sent to a waveform recorder for computer interfacing and to an oscillograph for paper recording. The waveform recorder was used as a discriminator to determine the occurrence of heartbeats and a microcomputer measured and recorded the intervals between heartbeats.

The electric stimulation was provided by the discharge of a capacitor triggered to electrodes on the surface near the head and tail of the fish. The capacitor was charged by a power supply at a level (approximately 6 V) which caused a temporary increase in the heartbeat interval upon application.

The experiment was directed by a microprocessor-based controller (Abrahamson, 1987). The controller initiated the recording of the heart rate, switched on the conditioned stimulus (CS), administered the shock, and determined the random time interval between trials. The level of the scattered signal was adjusted by the experimenter.

During a trial, the heartbeat intervals were recorded for 20 sec. prior to the presentation of the conditioned stimulus (CS), the simulated scattered ambient noise. Then intervals were recorded for the 6 sec. duration of the CS. Concurrent with the termination of the CS, the fish was given the unconditioned stimulus (US), an electric shock. The heart rate was also monitored after the US to check for skipped heartbeats.

The fish was first trained with the CS at a 'loud' level until a consistent conditioned response (CR) was obtained. A conditioned response was defined as a heartbeat interval during the CS of at least twice the standard deviation plus the mean of the resting heart rate prior to the CS. Threshold was the sound pressure level at which the fish showed a CR to 50 percent of the trials at that level. After one threshold was determined, the spherical transducer was moved to a new position.

The sound pressure levels for the ambient and scattered signals were measured by replacing the fish with a hydrophone positioned in the same location as the fish's ear. The ambient noise produced by the J-9 was measured first with a spectrum analyzer, then threshold levels for the scattered ambient noise were recorded as a function of range from the hydrophone.

The scattered noise pressure thresholds are plotted as a function of range in Figure 8. The solid line represents the level of the background noise source (J-9). The range given is the distance from the center of the fish's ears to the center of the transducer in the

horizontal plane. The shortest range tested was limited by the physical size of the fish and the hydrophone.

The velocity and pressure signal-to-noise ratios are shown in Figure 9. The particle velocity of the sound was calculated using the nearfield relation between the pressure and velocity for spherical waves. Note that the velocity S/N is independent of range at roughly 20 dB. A constant velocity S/N corresponds well with the idea that velocity is the adequate stimulus for the otolithic organs.

These preliminary results indicate that the goldfish was able to sense a filtered noise signal in broadband ambient noise. Therefore, the fish may be capable of sensing the scattered ambient noise from the swimbladder of another fish. It is not known whether the fish was responding to the acoustic pressure or the particle motion. Although the simulated scattered signal was centered around a frequency (700 Hz) thought to be in the realm of pressure sensitivity at threshold (Fay and Popper, 1974), the constant velocity signal-to-noise ratio suggests that velocity was the stimulus.

PROPOSED RESEARCH

The goals of the proposed research include (1) determining the characteristics of noise scattered by the swimbladder of the goldfish and the oscar (*Astronotus ocellatus*), a nonostariophysine, (2) developing a method to reproduce the scattered signal using signal generators and underwater transducers, and (3) measuring the ability of the fish to discriminate this signal from simulated ambient noise. Both a hearing specialist (goldfish) and a fish without any structural hearing adaptation (oscar) will be tested to determine the functional significance of the mechanical coupling between the swimbladder and the inner ear. It has been proposed that fish with poor coupling between the swim bladder and inner ear are not able to discriminate frequency or extract signals from noise as well as fish with good coupling (Rogers, et al., 1988).

Swimbladder Resonance

The NIVAMS will be used to measure the frequency response of the swimbladders of the goldfish and the oscar. At the present time, target motion in the test tank is normalized with acoustic particle motion calculated from pressure field measurements. The calculations are based on Euler's equation in one dimension, which may not be justifiable in the standing wave field of the test tank. An attempt will be made to directly measure the acoustic particle motion in the test tank using either a differential laser Doppler velocimeter (Vignola, 1990) or a FotonicTM optical displacement system.

The swimbladder resonance data will be compared with available theoretical models (Andreeva, 1964; Love, 1978) and other experimental data (McCartney and Stubbs, 1971; Chapman and Sand, 1974; Lovik and Hovem, 1979) to determine the proper signal necessary to mimic the scattering by a fish.

Response to Scattered Ambient Noise

The psychoacoustic setup will be modified in several areas to provide a more versatile system with easier operation. Improvements will be made in both the system hardware and software and the experimental procedure.

First the test tank will be replaced with a larger aquarium (48" x 30" x 18") to allow a greater separation of the fish and the transducer generating the simulated scattered signal. This tank will be decoupled from ground vibrations by air-spring isolators to flatten the frequency response.

The microprocessor-based controller will be removed. The experiment will be driven by a microcomputer with the controller's internal relays replaced by a GPIB switch control device, and a programmable attenuator will be used to adjust the level of the scattered signal. Custom software will be written to run trials, record and reduce data, and direct the experiment, reducing the need for operator involvement. The computer will determine auditory detection capabilities by using the up-down staircase method for threshold tracking.

To characterize the acoustic level in the test tank, both pressure and velocity data will be taken. The former will be measured with a hydrophone and the later the same velocimetry method used in the previous experiment.

Once the system is completed, thresholds for the scattered signal will be measured in both the goldfish and the oscar as a function of range and direction in the horizontal plane and the center frequency and bandwidth of the scattered signal. This data will then be compared to the model of Rogers (1986).

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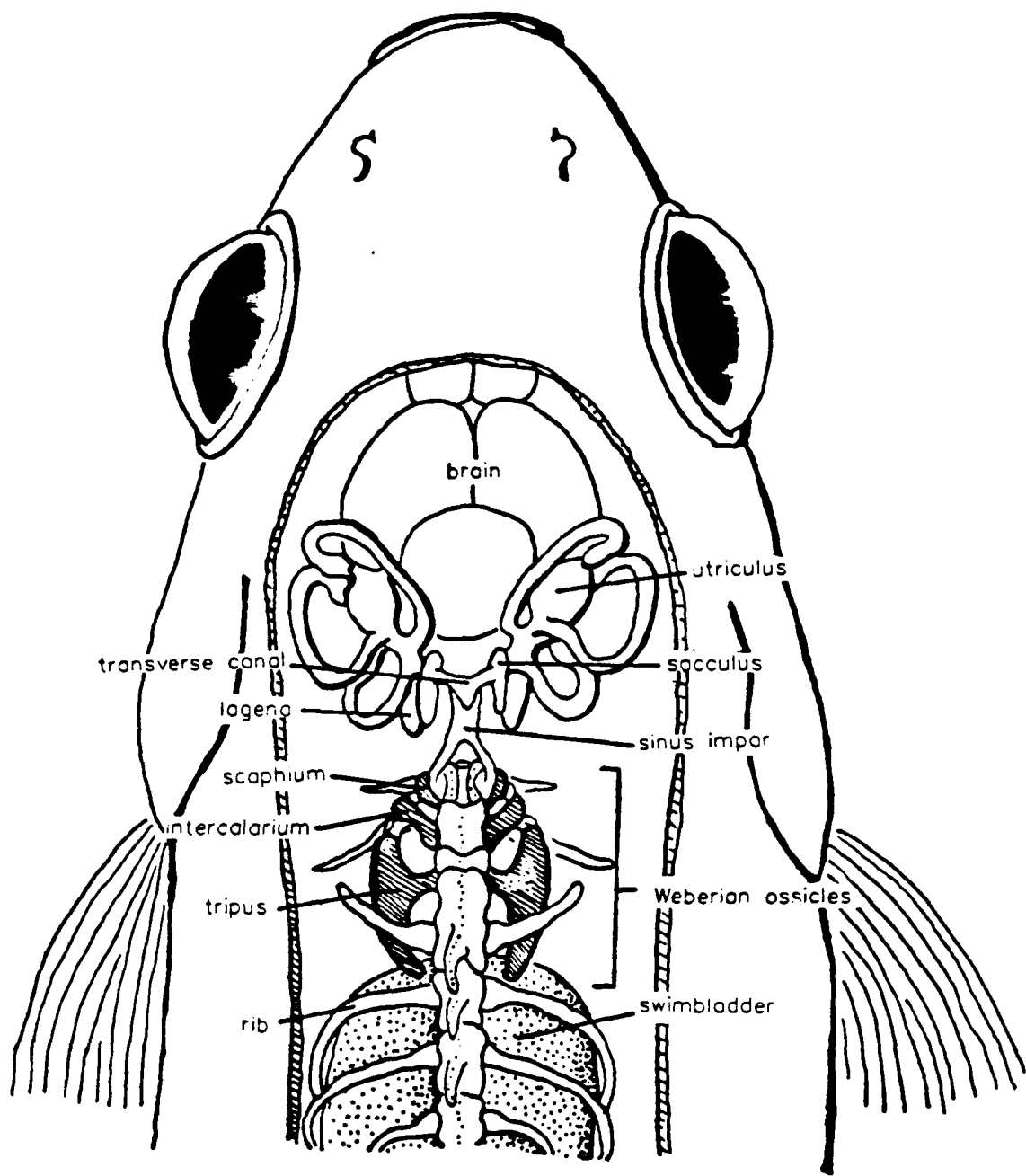


Figure 1. The layout of the swimbladder, Weberian ossicles, and inner ear in an Ostariophysian fish. (From Popper and Coombs, 1980.)

Carassius
Auratus

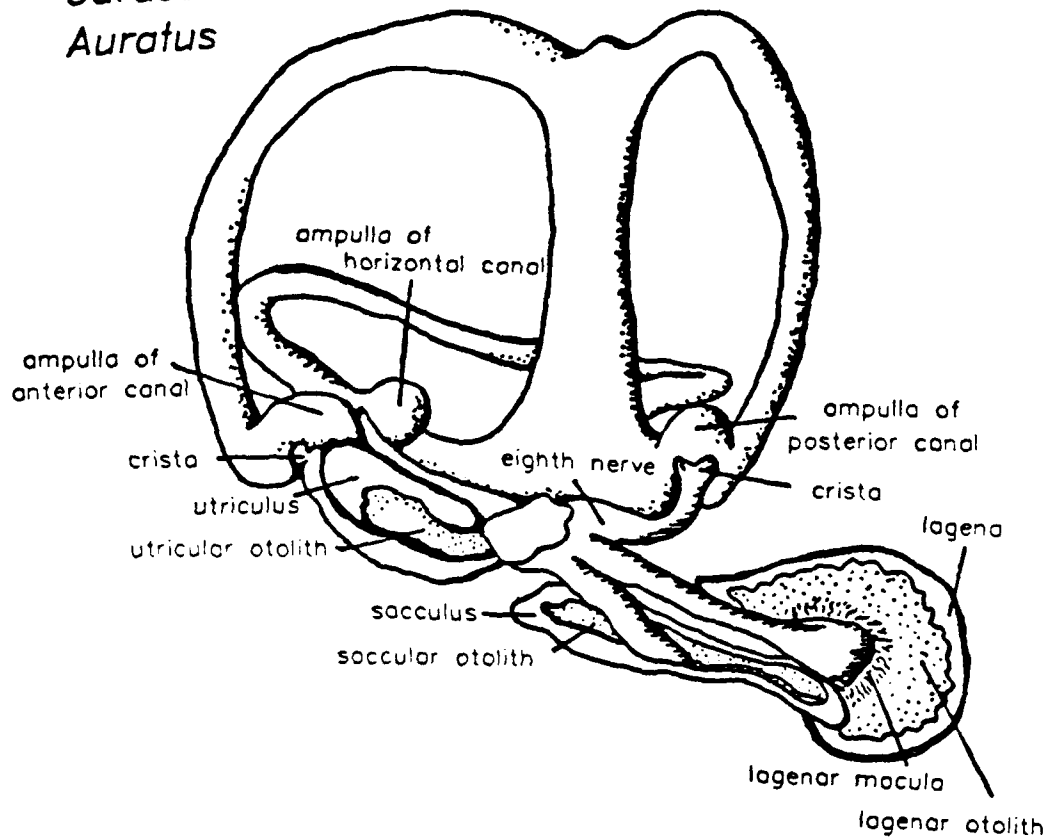


Figure 2. The ear of the goldfish, *Carassius auratus*.
(From Popper and Coombs, 1980.)



Figure 3. A scanning electron micrograph of the hair cell cilia on the saccular macula. The single kinocilium (K) is the longest, with the stereocilia decreasing stepwise in rows of equal height away from it. (From Fay and Popper, 1984.)

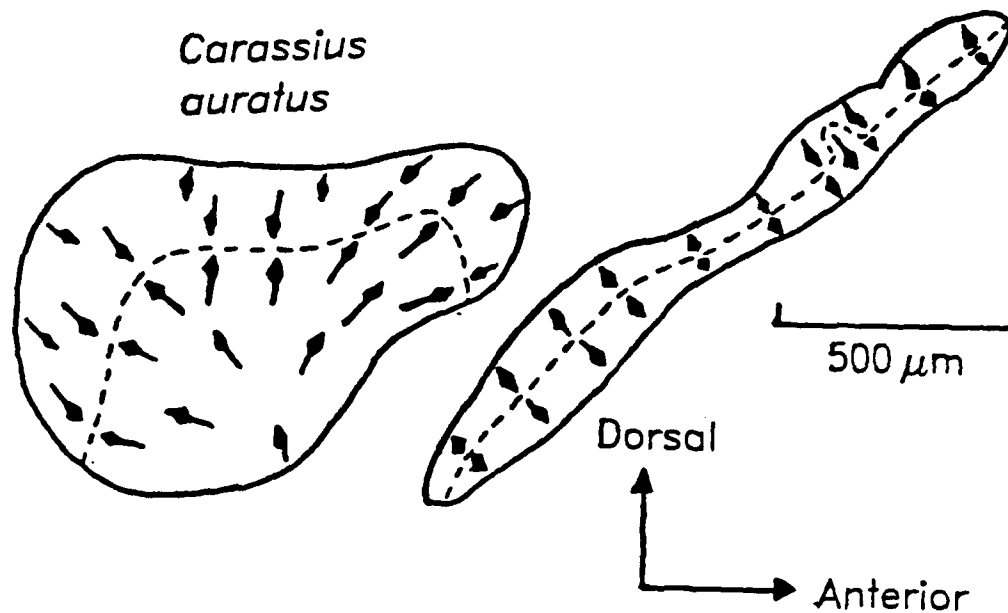


Figure 4. Orientation patterns of the hair cells on the lagena (left) and saccule (right) of the goldfish. Although shown in two dimensions, the macula are actually curved. The arrows indicate the direction of orientation of the kinocilium. (From Popper and Coombs, 1980.)

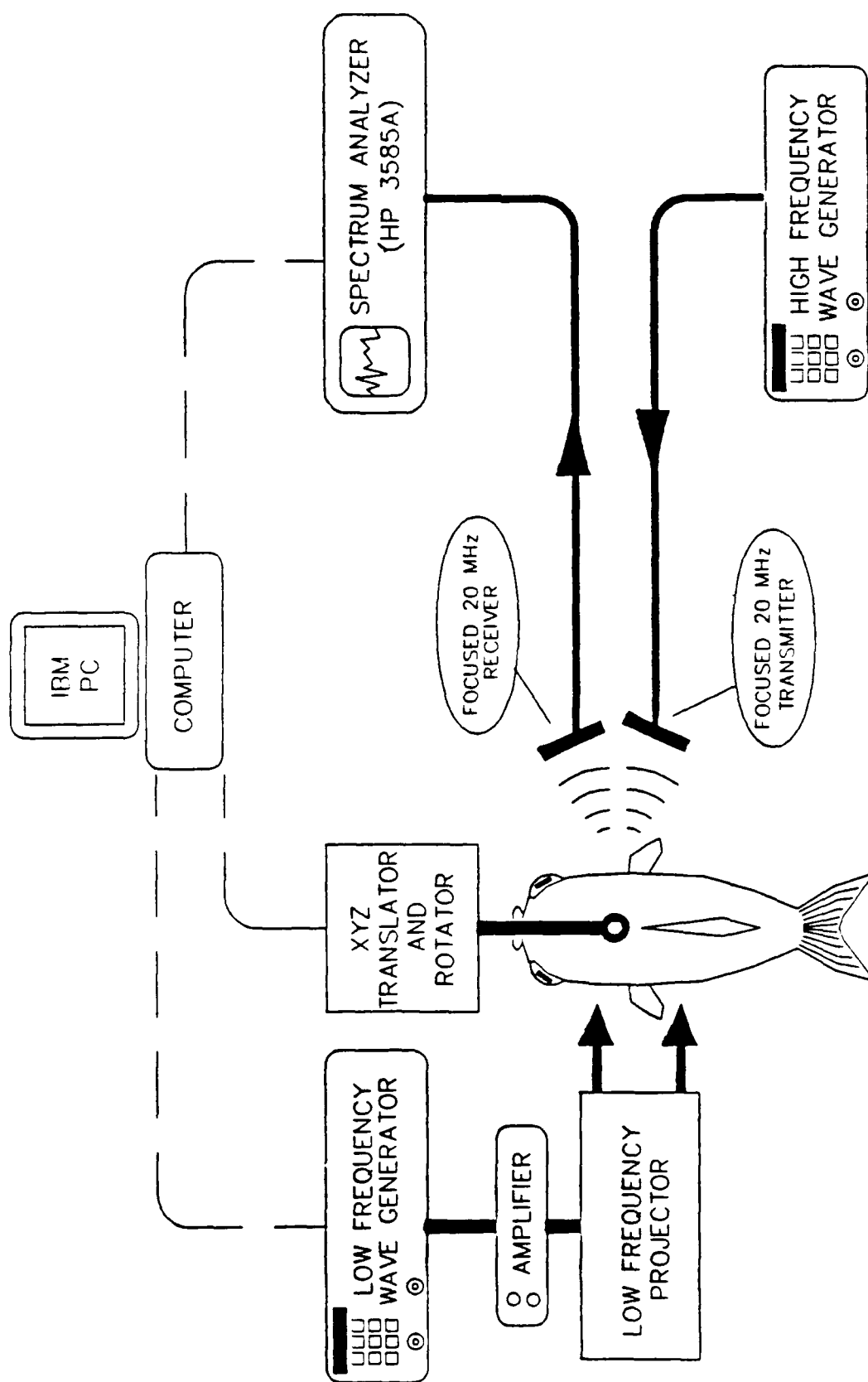


Figure 5. Non-Invasive Vibration Amplitude Measurement System (NIVAMS).

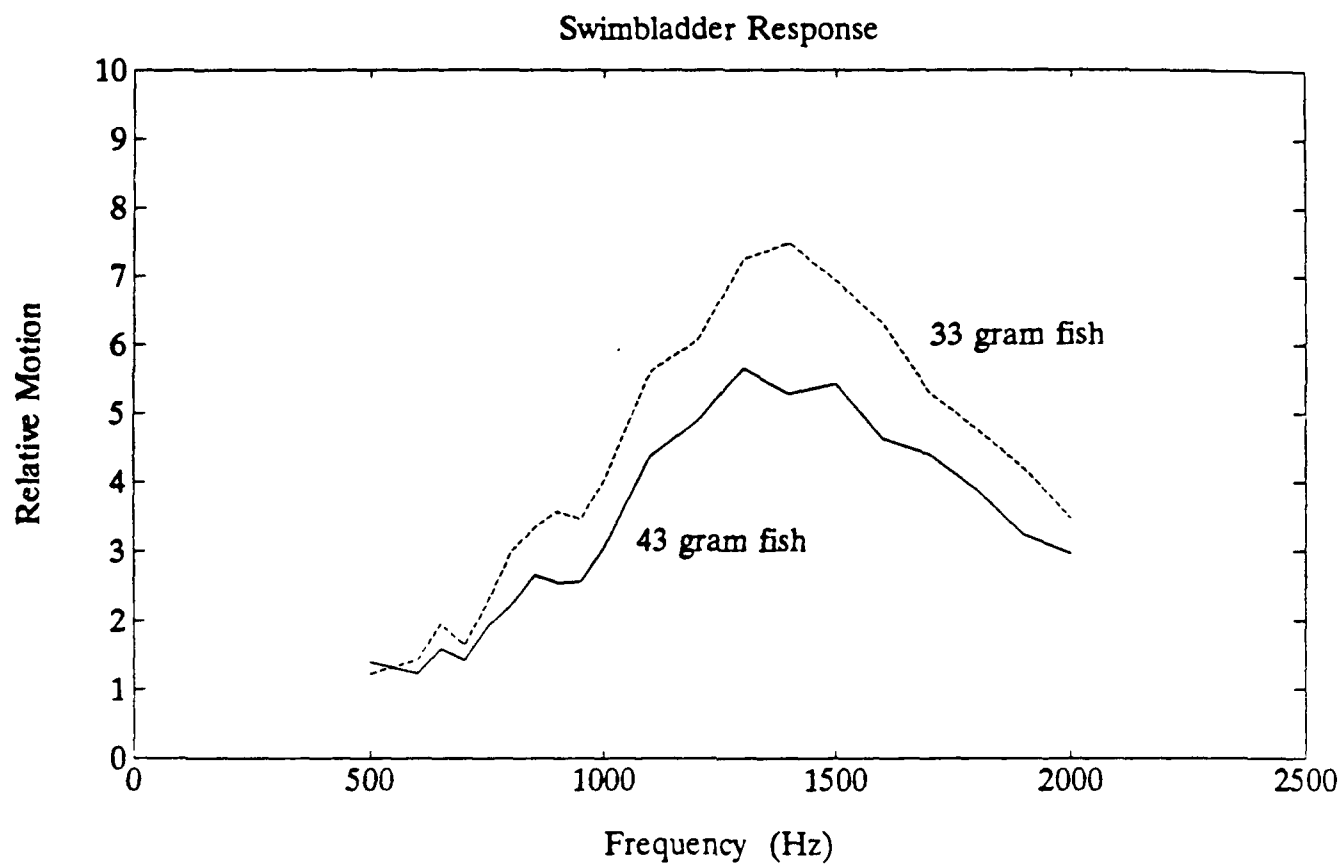


Figure 6. Frequency response of the swimbladders of two goldfish. The vertical axis represents relative motion, which was calculated as the ratio of the motion of the swimbladder to the acoustic particle motion.

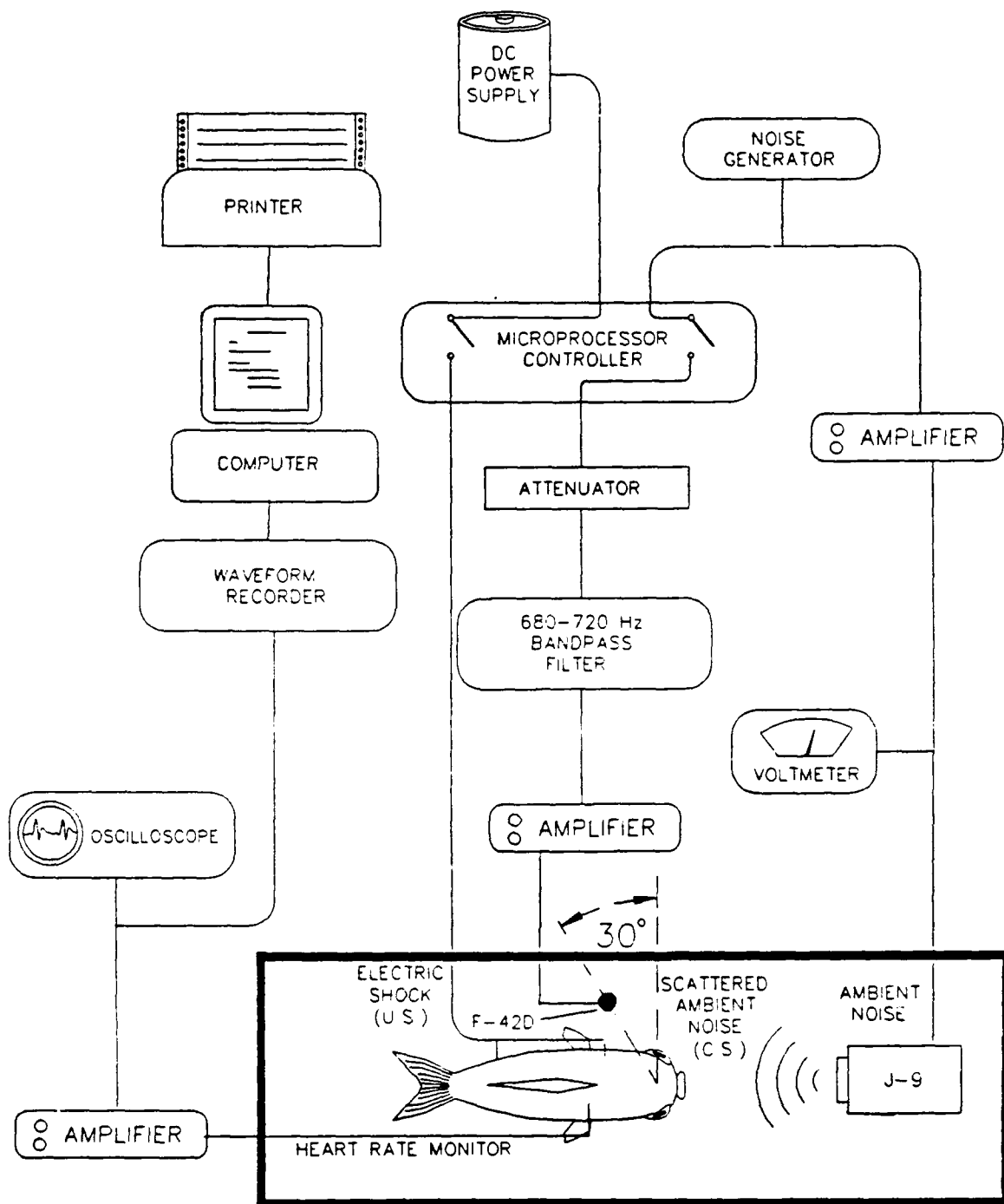


Figure 7. Scattered ambient noise experiment station.

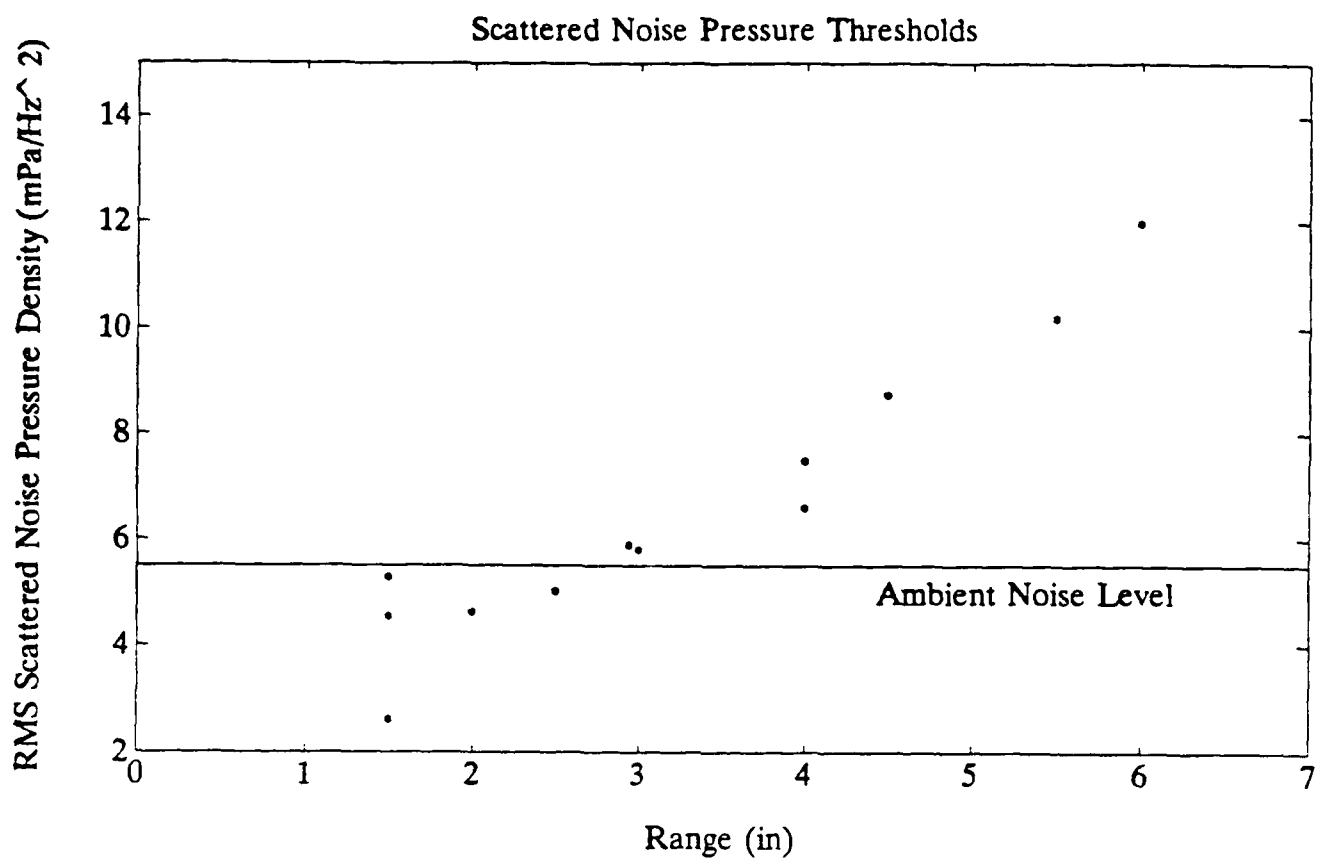


Figure 8. Scattered noise pressure threshold.

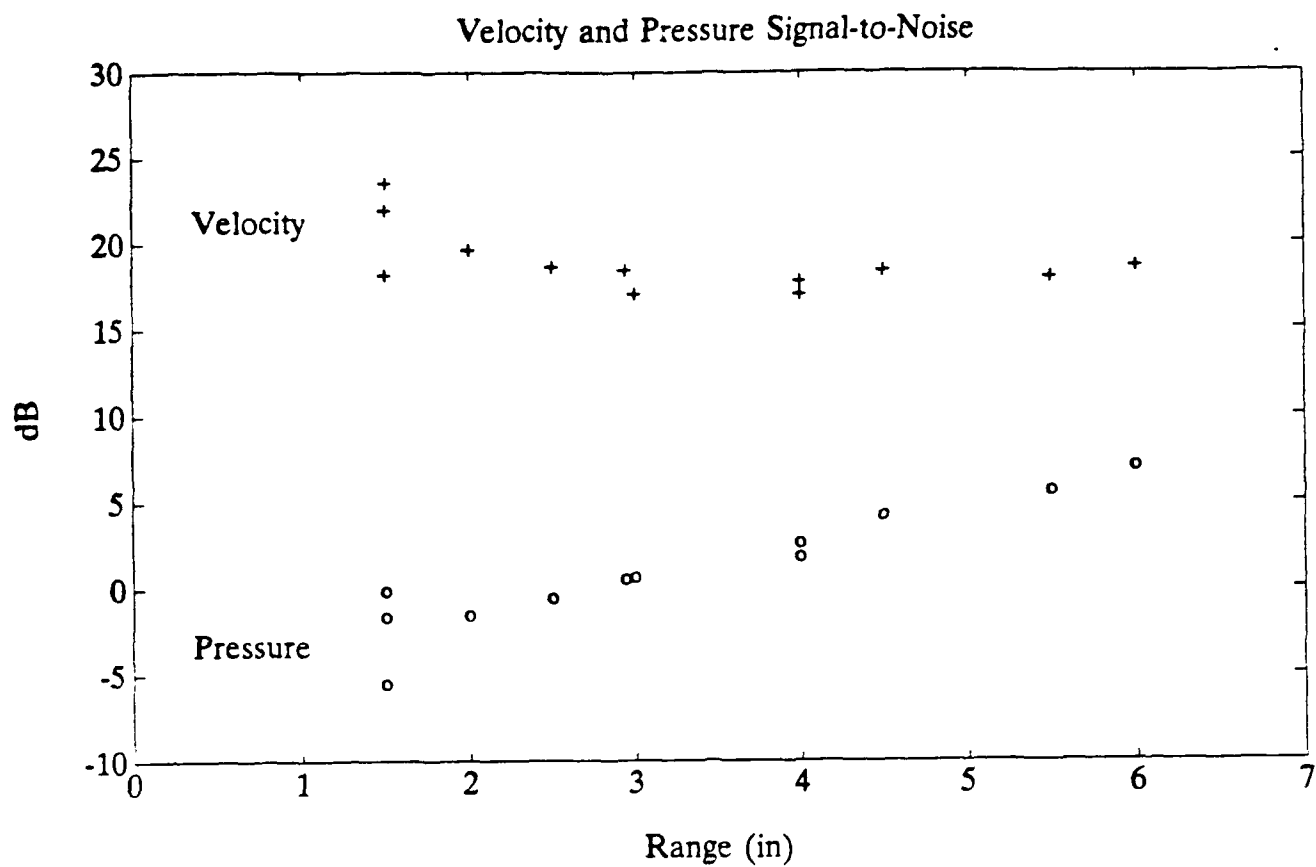


Figure 9. Velocity and pressure signal-to-noise at threshold.